SOME ASPECTS OF BEHAVIOR OF OYSTERS AT DIFFERENT TEMPERATURES

V. L. LOOSANOFF

U. S. Fish and Wildlife Service, Milford, Conn.

The oyster, *Crassostrea virginica* Gmelin, is a sedentary mollusk which must pump definite quantities of water through its gills, to obtain the food and oxygen necessary for its existence, and to get rid of the waste products. The stream of water created by a pumping oyster can easily be seen if the latter is kept in a shallow tray in water just deep enough to cover it. Even casual observations will show that the quantity of water pumped by an oyster changes from time to time, and that different oysters may pump at different rates.

In keeping oysters under laboratory conditions it is, obviously, of advantage to know the approximate quantity of water needed for their normal existence. The same information is of practical use to oyster cultivators in deciding the number of oysters that can be planted in a certain area to achieve the best growth. Furthermore, because of the recent progress in the artificial propagation of bivalves (Loosanoff and Davis, 1950; Loosanoff, 1954), which is now leading to mass production of clams and oysters under hatchery conditions, and because of the recent interest in the utilization for shellfish culture of small, salt water ponds, where annual fluctuations in temperatures may be great, extending in some regions from nearly 0.0° to 32.0° C. or even higher, a more complete knowledge of the behavior of the mollusks within this temperature range is needed. Finally, the differences in the rates of water pumping at the same temperatures by oysters from different geographic areas may be used as the criterion to ascertain the existence of different physiological races.

Studies of various aspects of filtration of the filter-feeding invertebrates, including oysters and closely related mollusks, have been made by many investigators. Comprehensive reviews of several hundred articles on these subjects were recently offered by Verwey (1952) and Jørgensen (1955); therefore, only those dealing directly with rates of water pumping by bivalves, especially oysters, will be referred to here.

The first comprehensive studies of the rate of pumping of the American oyster, *C. virginica,* at different temperatures were made by Galtsoff (1928a, 1928b). He used two methods. The first, the so-called "tank method," was designed primarily to collect the water after it had passed through the gills. The second or "carmine method" was devised to measure the rate of movement of the column of water flowing from the exhalant chamber through a glass tube. Galtsoff concluded that the maximum flow of water produced by an adult oyster, three to four inches in length, was 3.9 liters per hour at a temperature of 25.0° C. Galtsoff's conclusions were challenged by Nelson (1935, 1938) who considered these figures too low and thought that the methods used by Galtsoff unfavorably affected the experimental animals. Nelson, therefore, believed that Galtsoff's data did not truly present the normal activities of oysters. Nelson (1935) also reported that, instead of the 3.9 liters per hour indicated by Galtsoff as the maximum quantity of water that can be pumped by an oyster, some of the animals in his experiments pumped water at the rate of approximately 26.0 liters per hour. In our own work, we have recorded pumping rates of individual oysters as high as 34.0 liters per hour, *i.e.,* about ten times greater than Galtsoff's maximum (Loosanoff and Nomejko, 1946).

Most of Nelson's observations, as well as ours and those of several other investigators, were made, however, while studying various aspects of the physiological behavior of oysters and not during the studies devoted primarily to the evaluation of the effects of temperature upon their pumping rate. Since the need of more complete information on this subject still existed, the experiments discussed in this paper were conducted.

I wish to express my appreciation to Charles A. Nomejko for tabulating some of the data and for preparing photographs of the kymograph records, to Barbara J. Myers for the statistical treatment of the data used in this article and to Rita S. Riccio for her help in preparing the manuscript.

Methods

Only Long Island Sound oysters were used in these studies. For the sake of uniformity, they were selected to approximate the following standards: length—between 100.0 and 110.0 mm.; width—between 80.0 and 85.0 mm.; depth—between 30.0 and 35.0 mm.; and volume—between 85.0 and 100.0 cc. Before the oysters were used they were conditioned for several days at the temperature to be employed in the experiment.

The method for measuring the rate of flow of water through the gills of the oysters was based on the suggestions and apparatus of Moore (1910), Galtsoff (1926) and Nelson (1936), and was fully described in our article on feeding of oysters in relation to different concentrations of micro-organisms (Loosanoff and Engle, 1947). Here it is sufficient to mention that the so-called "rubber apron" method interfered in no way with the normal activities of the oysters and allowed us to collect and measure accurately the quantities of water pumped by them. Both the rate of pumping and the shell movements of the experimental oysters were continuously recorded by kymographs.

The temperature range covered by these experiments extended from about 0.0° to 38.0° C. The temperatures were usually maintained within ± 0.5° C., and the temperature intervals were 2.0° C. apart. The salinity of the water was usually about 27.0 p.p.t. and the pH, about 7.7.

In all these experiments the oysters were kept in running water, a condition which assured a more normal behavior than if the oysters had been confined to a small container repumping, time after time, the same water which, eventually, could become heavily laden with excretory products. The periods of observation extended from five to seven hours. Therefore, the conclusions offered here refer to these comparatively short periods, and the rates of pumping, as found in these experiments, would not necessarily be representative of longer exposures.

Results

Our studies, an abstract of which has already been offered (Loosanoff, 1950), consisted of 478 individual observations. However, because many oysters either did not open at all or opened but did not pump water, the conclusions are based, actually, on 337 experimental records (Table I).

The lack of activity, as could be expected, was virtually confined to the lower temperatures. Below 2.0° C. only one of eight oysters pumped. It opened its shells when the temperature was only 1.2° C. and, regardless of the somewhat irregular and feeble shell movements, it produced a weak but, nevertheless, real flow of water. The ability to pump water at low temperature was also recorded for another individual that pumped a relatively large quantity of water at a temperature between 2.7° and 3.3° C. and maintained such a pumping rate for several hours (Fig. 1). Hopkins (1933) working on the closely related species, *Crassostrea gigas,* also reports that the distinct flow produced by this mollusk was observed and recorded at as low a temperature as 2.6° C.

Table I

Average rates of water pumping, in cc. per hour, of groups of oysters subjected for approximately six-hour periods to temperatures ranging from 0.0° to 38.0° C.

Temperature intervals ° C.	Number of oysters			Pumping rate	
	Total	Open	Pumping	Average	Maximum
0.0– 2.0	8	2	1	113	—
2.1– 4.0	52	22	1	863	1,020
4.1– 6.0	28	14	5	180	266
6.1– 8.0	20	12	6	495	1,197
8.1–10.0	36	21	16	763	1,594
10.1–12.0	36	24	22	2,914	4,303
12.1–14.0	32	25	22	3,902	5,409
14.1–16.0	28	27	26	4,344	5,787
16.1–18.0	21	21	21	9,083	11,583
18.1–20.0	33	33	33	7,020	9,773
20.1–22.0	42	42	42	9,802	13,341
22.1–24.0	24	24	24	7,795	10,802
24.1–26.0	14	14	14	9,537	12,635
26.1–28.0	20	20	20	9,366	11,569
28.1–30.0	24	24	24	12,983	15,155
30.1–32.0	19	19	19	11,813	16,253
32.1–34.0	20	20	20	8,948	12,856
34.1–36.0	17	17	17	2,785	4,201
36.1–38.0	4	4	4	2,449	3,884
Total	478	385	337	—	—

Since some of the oysters exposed to very low temperatures not only kept their shells open, but also pumped small quantities of water, experiments were devised to ascertain whether these oysters were ingesting food under such conditions. They were conducted during February when the temperature of Milford Harbor water is at its lowest. Three-year-old oysters, brought from outdoors, were placed into individual glass dishes which, in turn, were placed in shallow, white enamel trays of cold, running sea water. A cold culture of deep-green *Chlorella* was added as a biological indicator, to appear in the feces if the oysters fed.

Of the 90 oysters kept for 24 hours at a temperature ranging between 2.0° and 3.0° C., only one individual passed a small quantity of true feces. However, about 15 per cent of the oysters formed pseudo feces. When the temperature was kept between 3.0° and 4.0° C., approximately one-half of the 90 oysters formed pseudo feces, but only a single case of true feces was observed. Thirty oysters from this group were opened and examination showed that in all but one case their stomachs were empty and crystalline styles absent. The same results were obtained when the temperature ranged between 4.0° and 5.0° C. However, when the temperature was kept between 5.0° and 6.0° C., 11 of the 90 oysters expelled true feces, two of them in large quantities, and over 75 per cent formed pseudo feces.

These experiments have shown that, although feeding of oysters below 5.0° C. occurs only as an exception, a relatively high percentage may form pseudo feces,

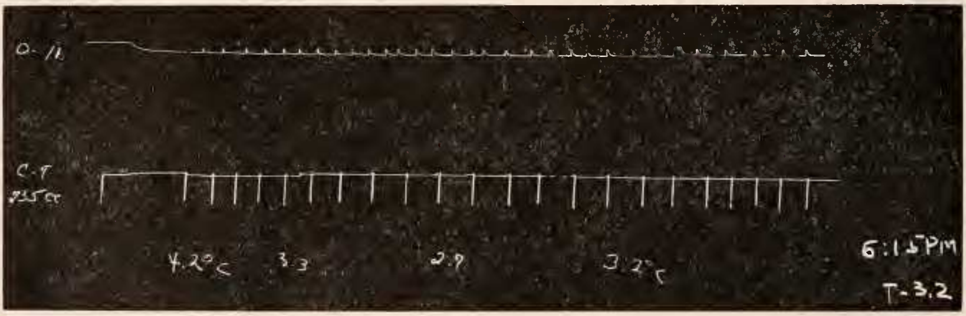

FIGURE 1. Kymograph record of shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to water temperature ranging between 2.7° and 4.2° C. from 11:45 A.M. to 6:15 P.M. Each vertical mark of the second line designates the discharge of 235 cc. of water pumped by the oyster.

even at a temperature as low as 2.0° or 3.0° C. The explanation as to why pseudo feces can be produced at lower temperatures than true feces lies, perhaps, in the observation made by Galtsoff (1928a), that the frontal cilia are able to transport the particles along the surface of the gills at a temperature of only about 3.0° C., while the lateral cilia can, as a rule, produce a current only when the temperature of the surrounding water is about 5.0° C.

The observations that some oysters feed at low temperatures are supported by those made by Nomejko and Chanley of Milford Laboratory who, in conducting a survey in Long Island Sound on March 11, 1954, dredged an oyster which possessed a well-developed crystalline style and contained food in its stomach. The temperature of the water at that time was approximately 3.0° C.

Our studies also showed that many oysters which open at the lower temperature may move their shells steadily, but pump no water. Twenty-one of the 22 oysters which opened at temperatures between 2.1° C. and 4.0° C. behaved in this manner (Table I).

Our observations lead us to believe that Galtsoff's (1928a) statement, that in

C. virginica no current is produced and no feeding occurs at or below 5.0° C., should be qualified because this rule, obviously, does not apply to all individuals. His generalizations, nevertheless, remain applicable to the large majority of the oysters.

The average and maximum rates of pumping of the groups of oysters within each temperature interval are given in Table I. In general, the rate of pumping remained low until the temperature interval of 8.0°–10.0° C. was reached. After that, and until the temperature of about 16.0° C. was attained, it showed a moderate increase. No radical fluctuations were recorded, however, between this point and

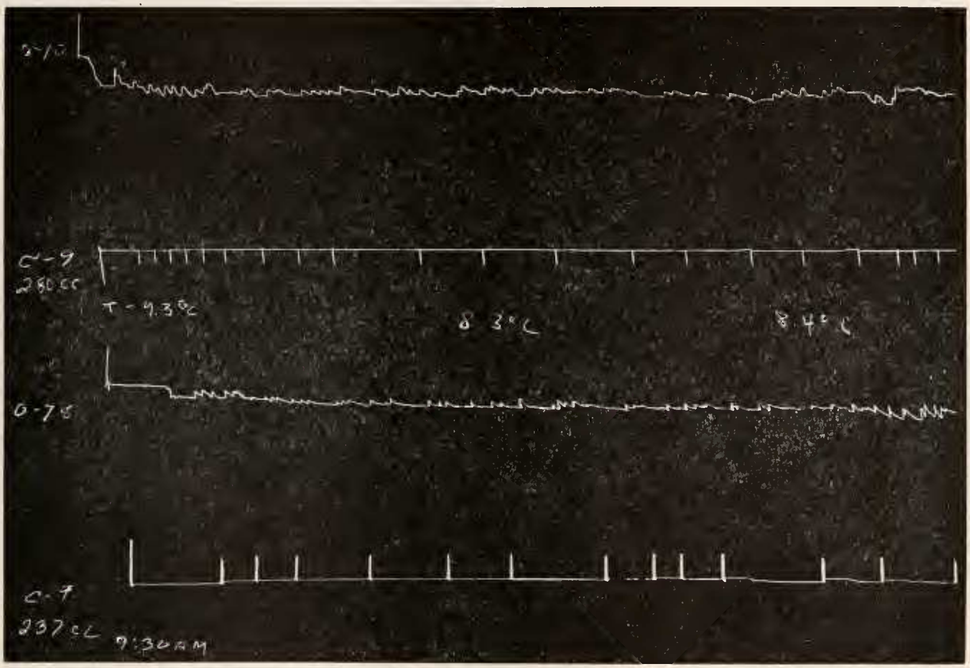

FIGURE 2. Kymograph record showing shell movements (1st and 3rd lines) and rates of pumping (2nd and 4th lines) of two oysters exposed to temperatures ranging from 8.3° to 9.3° C. from 9:30 A.M. to 2:15 P.M. Each vertical mark on the second line designates the discharge of 280 cc. of water pumped by the oysters, while each mark of the fourth line shows the discharge of 237 cc.

the temperature of 28.0° C. The greatest average rate of pumping, 12,983 cc. per hour, was recorded between 30.0° and 32.0° C. After passing the maximum, the relatively fast pumping continued until about 34.0° C. and then abruptly decreased.

Some aspects of pumping at different temperatures are demonstrated in this article by photographs of the kymograph records showing both shell movements and rates of pumping. At comparatively low temperatures, such as 8.0° to 9.5° C., shell movements of the oysters may not be well defined and the amount of water pumped through the gills remains relatively small (Fig. 2). As the temperature of the water increases toward the optimum range, many oysters begin to display the type of shell movement called "staircase" or "treppe," which some students think is due to chemical stimulation affecting the experimental oysters with a gradual increase in intensity. We hesitate to accept this as a satisfactory explanation of the phenomenon. In many of our experiments the "staircase" shell movement occurred in normal-feeding oysters, although, as shown in Figure 3, this type of shell movement was often observed soon after the oysters opened and began to pump.

In our studies usually two or four oysters were under simultaneous observation, receiving the same amount of water, connected to the same kymograph and treated identically in all other respects. Yet, in many instances, including the one shown in Figure 4, the "staircase" type of shell movement was displayed at any given time

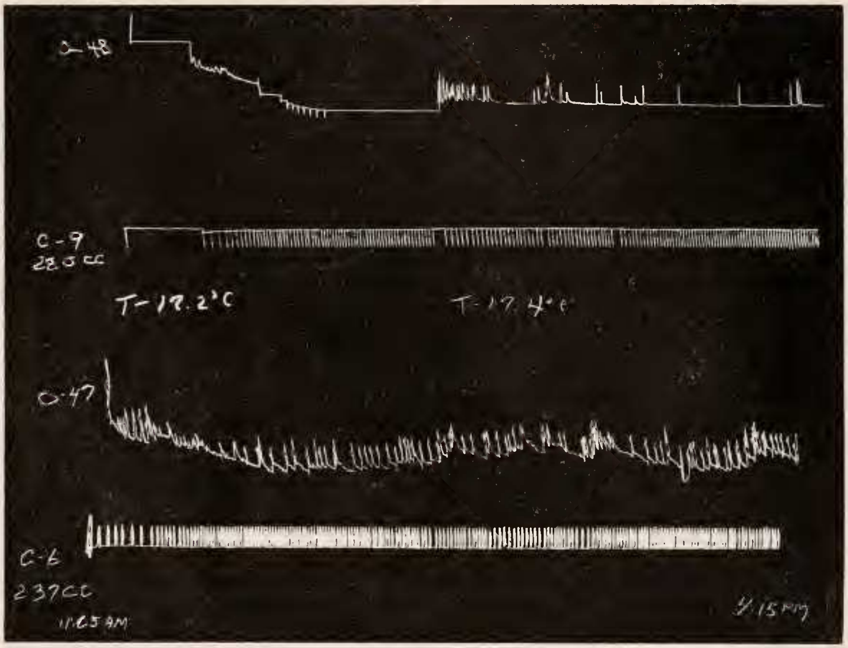

FIGURE 3. Kymograph record showing shell movements (1st and 3rd lines) and rates of pumping (2nd and 4th lines) of two oysters exposed to temperatures ranging from 17.2° to 17.4° C. from 11:05 A.M. to 4:15 P.M. Each vertical mark on the second line designates the discharge of 280 cc. of water pumped by the oysters, while each mark of the fourth line shows the discharge of 237 cc.

by one oyster only. This clearly indicated that it was not a specific chemical in the water that was responsible for stimulation of the oysters leading to this type of shell movement. Obviously, further physiological studies are needed to explain the cause of the "staircase" type of shell movement.

Within the favorable temperature range many oysters were recorded as pumping over 20,000 cc. per hour, and several individuals were observed pumping at the rate of 25,000 to 29,000 cc. per hour. The maximum rate of pumping for an individual oyster was recorded at a temperature ranging between 24.1° and 24.5° C. when one of the two oysters (indicated as O-10 in Figure 4) averaged 37,446 cc. per hour for a period of about five hours, and for several shorter periods of about 15 minutes pumped at the rate of about 40,000 cc. per hour. Because of such a rapid rate of pumping the strokes of the needle on the kymograph drum, each representing a discharge of 237 cc. of water, were made so close to each other that the record appeared blurred. Fortunately, by employing the low power of a dissecting microscope the strokes could be accurately counted and the record properly analyzed and evaluated.

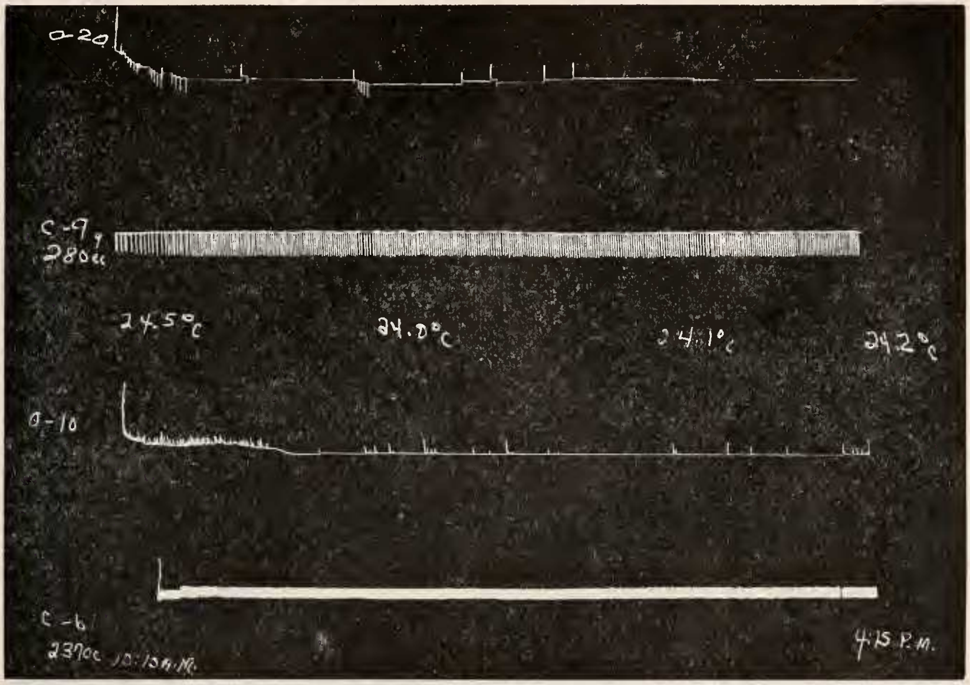

FIGURE 4. Kymograph record showing shell movements (1st and 3rd lines) and rates of pumping (2nd and 4th lines) of two oysters exposed to temperatures ranging from 24.0° to 24.5° C. from 10:10 A.M. to 4:15 P.M. Each vertical mark on the second line designates the discharge of 280 cc. of water pumped by the oysters, while each mark of the fourth line shows the discharge of 237 cc.

Incidentally, studies of many of our records indicate that often, at favorable temperatures, when the shells of the oysters are open and relatively motionless, large quantities of water are pumped. This is well demonstrated by the activities of the two oysters in Figure 4, one of which pumped the record quantities of water and the other also pumped at a rapid rate.

Almost immediately after passing the temperature level of 32.0° C. and, actually, in some instances, even between the temperatures of 31.1° and 32.0° C., certain signs began to appear, indicating that some oysters were being unfavorably affected. Among these signs were changes in the character of the shell movements, complete closing of the shells and cessation of pumping at frequent intervals, and a reduced rate of pumping even during the period when the shells remained open. Within the range of 34.1° to 36.0° C. these symptoms became more pronounced (Fig. 5).

Above 36.1° C. the type of shell movement became even more abnormal, and the oysters stayed closed approximately two-thirds of the time exposed.

To determine the significance of the differences in the average pumping rates of oysters at the different temperature intervals, a simple analysis of variance was employed. It was found unnecessary to compute all the *t*'s between adjacent temperature intervals. The same objective could be achieved by using a simple analysis of variance to test for homogeneity within each of the several apparently homogeneous levels, and also to test for the significance of the differences between these levels. These tests showed homogeneity within the following five temperature intervals: 4.1°–10.0° C., 10.1°–16.0° C., 16.1°–28.0° C., 28.1°–34.0° C., and 34.1°–38.0° C. The means for these five levels are shown in Figure 6 and are 593; 3,714; 8,727;

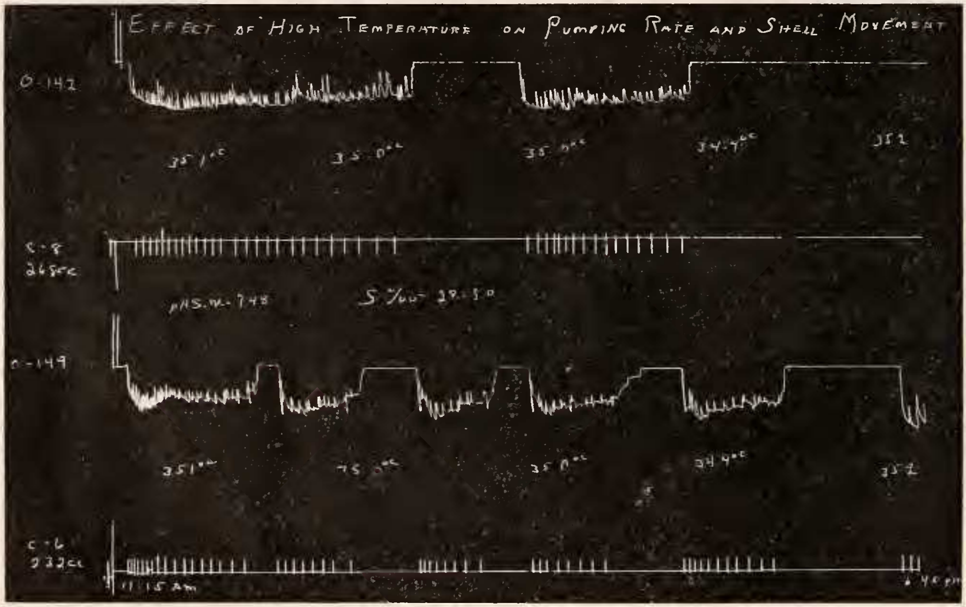

FIGURE 5. Kymograph record showing shell movements (1st and 3rd lines) and rates of pumping (2nd and 4th lines) of two oysters exposed to temperatures ranging from 34.9° to 35.2° C. from 11:15 A.M. to 6:40 P.M. Each vertical mark on the second line designates the discharge of 268 cc. of water pumped by the oysters, while each mark of the fourth line shows the discharge of 232 cc.

11,365 and 2,762 cc., respectively. The analysis indicated, as expected from inspection of this figure, that there were highly significant differences among these five levels. It was concluded, therefore, that the average pumping rate can be described as being related to these differences.

There are ecological situations in nature where changes in the temperature of the water are frequent and rapid. Many small, shallow, salt water ponds, of the type that can be adapted to shellfish cultivation, may belong to this category. Oysters living in such ponds or other similar bodies of water may experience such changes in temperature, especially during early spring and late autumn when the temperature of the water may quickly cool off during the night, decreasing to almost

0.0° C., and rapidly rise during the daytime. The question that naturally arises for such a situation is, how are the oysters affected by such changes and do they resume normal pumping regardless of the rapid change in the temperature from nearly freezing to about 15.0° C. or even higher?

The first series of experiments designed to answer the above question was conducted in October. The oysters were brought from outdoor tide-filled tanks, where the temperature of the water was about 13.0° C. One-half of the oysters, which served as the control, were placed in an aquarium in which the water temperature

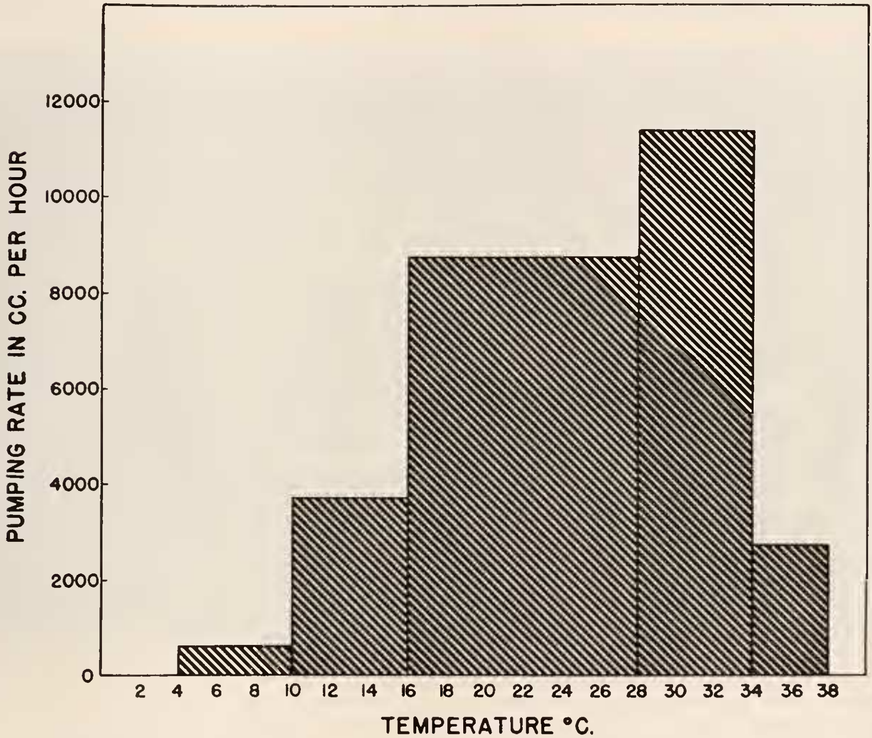

FIGURE 6. Mean rate of water pumping by oysters at five homogeneous temperature levels.

was kept at about 18.0° C. The other half were put in special containers in the refrigerator, where the temperature was about 3.0° C., and kept there from eight to 12 days. After this period at low temperature these oysters, as well as those serving as the control, were attached to kymographs. Extreme care was exercised during the handling to maintain the low temperature of the water for the refrigerated oysters. When the oysters of both groups were ready and attached to the kymographs a flow of water, about 18.0° to 20.0° C., was introduced simultaneously to all chambers, displacing the cold water surrounding the refrigerated oysters, and the behavior of all specimens was recorded from then on.

In a second series of experiments conducted in the middle of the winter (Fig. 7) the low-temperature oysters were not kept in the refrigerator but in the outdoor tanks where the temperature of the water was near 0.0° C. The oysters which were to serve as the control were, however, kept for three weeks in the laboratory at room temperature before being used in the experiments. In all other respects the methods used in the two series were the same. Altogether, in the two series of experiments, 33 control and 31 experimental oysters were used.

Student's *"t"* test was made to determine the significance of differences in the average pumping rate of the two groups. Because the "*t*'s" were far from significant, it was concluded that sudden upward changes in temperature, such as from 1.5° C. to about 18.0° C. (Fig. 7), had no significant effect on the pumping rate of the "cold water" oysters when such rate was compared with that of the control

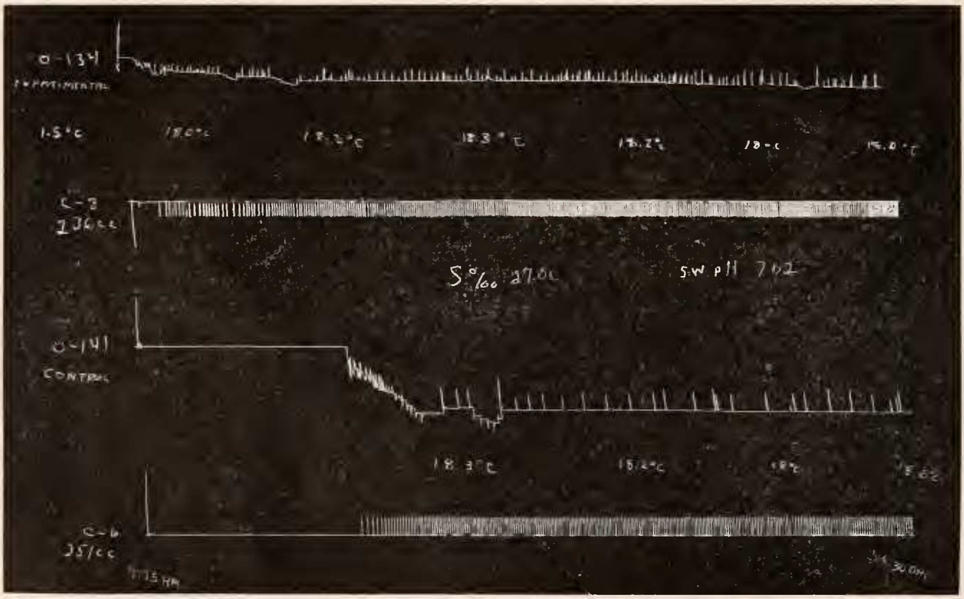

FIGURE 7. Kymograph record showing shell movements (1st and 3rd lines) and rates of pumping (2nd and 4th lines) of two oysters from 9:25 A.M. to 4:30 P.M. One, O-134, was exposed to rapid change of temperature from 1.5° to about 18.0° C., while the control oyster, O-141, was constantly subjected to the same temperature of about 18.0° C. Each vertical mark on the second line designates the discharge of 236 cc. of water pumped by the oysters, while each mark of the fourth line shows the discharge of 251 cc.

oysters. It was demonstrated, nevertheless, that there was a highly significant tendency of the oysters subjected to sudden changes from low to high temperature to open and pump almost immediately after the change was made, while the control oysters, as illustrated in Figure 7, usually required a much longer time to open their shells and begin pumping.

The results of these experiments differ from those of Galtsoff (1946) who, after keeping two oysters for 24 hours at 5.0° C. and then exposing them to a temperature of about 21.0° or 22.0° C., concluded that the shell movements of those oysters were abnormal and that they started to pump only on the third or fourth day after they had been placed in warmer water. We found no such abnormalities in the shell movements of the individuals used in our experiments (Fig. 7). Moreover, as already mentioned, the majority of our oysters previously kept in cold water opened and began pumping almost immediately, not after three or four days as found by Galtsoff. Our observations indicated, consequently, that the response of the oysters to a sharp and quick increase in temperature, from near 0.0° to about 15.0° to 20.0° C., is rapid and results in apparently normal pumping. The oysters, therefore, are physiologically well adapted to such changes which they, no doubt, often encounter in nature, for example, when living on the tidal flats where, at the autumn low tide, the night air may cool the water of the small pools containing the oysters almost to freezing, while the incoming tide may cover the same oysters with much warmer water.

Discussion

The rate of water pumping of different bivalves has been studied by a number of investigators. Among them, Jørgensen (1949) and Willemsen (1952) studied it in the common mussel, *Mytilus edulis;* Fox *et al.* (1937) and Rao (1953) worked on the closely related species, *M. californianus;* Willemsen (1952) also determined the quantities of water pumped by cockles, *Cardium edule;* Hopkins (1933, 1935) conducted extensive studies on the pumping of the Japanese commercial oyster, *Crassostrea gigas*, while Chipman and Hopkins (1954) determined the rate of water filtration by the common scallop, *Pecten irradians*. Most of these workers, except Hopkins, used the so-called indirect method based on a reduction of the number of particles or plankton organisms in suspension in the water in which the mollusks were kept. Hopkins used his own "cone" method by means of which he could determine only the relative rate at which the oysters pumped at different temperatures.

The most extensive observations on the rate of water transport were conducted on the American oyster, *C. virginica*. Except for Galtsoff's (1928a) pioneer experiments and Jørgensen's (1952) studies, investigators have used the direct or so-called "rubber apron" method, which permits measuring the actual quantities of water passed by oysters without interfering with their normal behavior. Most of these studies, however, including those of Loosanoff and Nomejko (1946), Loosanoff and Engle (1947) and Galtsoff *et al.* (1947), were made within relatively narrow temperature ranges not including the low or high temperature zones. Results of studies by Nelson (1935) and Loosanoff (1950), covering broader ranges, were presented only as brief abstracts.

As already mentioned, Galtsoff's (1928a) early experiments were criticized because the methods that he was then employing adversely affected the oysters (Nelson, 1938). Yet, regardless of the defects in his methods, Galtsoff, although giving rather low figures for the quantities of water pumped by oysters, indicated, nevertheless, quite correctly the general trend of the changes in the rate of pumping in relation to different temperature levels. For example, he observed that no feeding took place at 5.0° C. or lower. These conclusions, with the few exceptions demonstrated by our studies and by Hopkins' (1933) observations on the closely related species, still hold true for the majority of the population of *C. virginica* of northern waters. Galtsoff's observations that between 15.0° and 25.0° C. the fluctuations in the rate of pumping of individual oysters were small, strongly support the validity of our conclusions that between 16.0° and 28.0° C. the rate of pumping showed no marked fluctuation. Finally, his figures indicate a sharp drop in the rate of pumping after the temperature reaches and passes 34.0° C., as was also observed in our experiments.

Our observations showed that the highest average rate of flow of water through the gills of the oysters was achieved at about 29.0° C. (Table I). In this respect our results are in agreement with those of Nelson (1935) who determined that the maximum pumping in oysters occurs near 30.0° C. Our conclusions also resemble those of Galtsoff (1928b) that the optimum temperature for the mechanical activities of the oyster gills lies between 25.0° and 30.0° C. However, Galtsoff found that the maximum rate of pumping occurs at 25.0° C., somewhat lower than that recorded by Nelson (1935) or found in our studies. Nevertheless, considering Galtsoff's findings concerning the temperature at which the maximum activity of the oyster gills takes place, the three series of studies are in close agreement. Collier (1954) thinks, however, that even on the Gulf Coast the optimum temperature range for *C. virginica* lies between 15.0° and 25.0° C.

As to the maximum quantities of water pumped by *C. virginica,* there is considerable disagreement between the conclusions of the earlier workers, whose studies were reviewed by Galtsoff (1928a), and the more recent ones. The former estimated that oysters are capable of pumping only a few liters per hour. Wells (1926) gave the highest figure, advancing the opinion that at a favorable temperature oysters can average more than 7.5 liters per hour. His conclusions, however, were strongly challenged by Galtsoff (1928a), who expressed doubt that oysters can pump water at that rate.

Later investigators, who used the "rubber apron" method, have shown that the quantities of water pumped by oysters are much greater than those suggested by earlier workers. Nelson (1935) gives 26.0 liters per hour as the maximum quantity. Our maximum figure for a single oyster, as already mentioned, was 37,446 cc. for one complete hour, and an even higher rate was recorded for shorter periods. The maximum average hourly rate of pumping for a group of oysters was recorded within the temperature range of 28.1° to 30.0° C. and was 12,983 cc.; the maximum hourly rate, recorded between 30.1° and 32.0° C., was 16,253 cc. (Table I). Galtsoff *et al.* (1947) gave 9.6 liters as the average and 16.0 liters as the maximum hourly rate of water pumped by the oysters of York River, Va. Jørgensen's (1952) figures obtained by somewhat different methods are, nevertheless, very close to ours, being 11.0 and 15.5 liters per hour for the average and maximum rates, respectively. These figures attest the ability of the oysters to pump large quantities of water and indicate the importance of considering the water requirements of these mollusks in experimenting with them, or in their cultivation.

Summary

1. Some adult Long Island Sound oysters are able to pump water at a temperature as low as about 1.0° C. Oysters with crystalline style and food in their stomachs may occasionally be found in northern waters in winter.

2. Approximately 15 per cent of the oysters exposed to temperatures ranging from 2.0° to 3.0° C., and approximately 50 per cent of the oysters kept between 3.0° and 4.0° C. formed pseudo feces.

3. The average and maximum rates of pumping of the groups of oysters exposed to temperatures from 0.0° to 38.0° C. were determined. The rate remained low

under 8.0° C. Within the range from 8.1° to 16.0° C. the rate steadily increased. Between that point and about 28.0° C. the rate showed no marked fluctuation. A further increase was noted between 28.1° and 32.0° C. It is within this range that the maximum average rate of pumping of 12,983 cc. per hour was recorded. Between 32.1° and 34.0° C. the rate was also rapid. Beyond 34.1° C. the oysters showed a marked decrease in the rate of pumping and their shell movements were abnormal.

4. The maximum rate of pumping for an individual oyster averaging 37,446 cc. per hour was recorded at the temperature of about 24.0° C. For short periods of five to 15 minutes the rate of pumping of the same oyster exceeded 40,000 cc. per hour.

5. Statistical tests showed homogeneity of the rates of pumping within the following five temperature intervals: 4.1°–10.0° C., 10.1°–16.0° C., 16.1°–28.0° C., 28.1°–34.0° C. and 34.1°–38.0° C. The means for these five intervals were 593; 3,714; 8,727; 11,365 and 2,762 cc. per hour, respectively. Highly significant differences among these five levels were indicated by statistical analysis.

6. The rate of pumping of oysters kept at a temperature below 5.0° C. and then quickly changed to the higher temperature of 18.0° to 20.0° C. was virtually the same as the control oysters, thus indicating that the response of the oysters to such changes in environment and their adjustment to these changes are rapid.

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